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XXIII.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.* By THOMAS WILLIAMS, M.D. Lond., Licentiate of the Royal College of Physicians, formerly Demonstrator on Structural Anatomy at Guy's Hospital, and now of Swansea.

[With three Plates.]

[Continued from p. 57.]

Structure of the Branchiæ in the Lamellibranchiate Mollusks.

THE *mist* upon this branch of natural history which has survived the brightening science of a bright century may indeed refuse to be dissipated even by the achromatic microscope—the potent wand of the modern observer. That which the calm eye discerns with clearness, and the understanding interprets with confidence, though amplified many hundred diameters, is as likely to be an immutable objective truth as any "instance" within the sphere of the unassisted vision. Faith in the verity of microscopic facts is a fundamental article in the scientific creed of every living philosopher. The sphere of the naked vision is exhausted: another is opened by the microscope. Minute descriptions of subtle and complex structures, rendered possible only through its instrumentality, will prove of as great service in the hands of the future lawgivers of science, as the grosser narratives of the fathers of anatomy have already proved in the founding of the temple in which the high priests of natural theology now chant her service.

The branchial structures of the Mollusca have never yet been unravelled. The problem, though not impracticable, still awaits solution. The system of the gills is a conspicuous element in the molluscan organism. In apparent size they are considerable.

If function were expressed in numeric amount by the dimensions of the organs, the physiologist would assign to this class of animals a high degree of respiration. Minute structure is a factor in the estimate. The gills of the Lamellibranchiate mollusk are singularly and peculiarly formed: they admit of comparison in structural characters with no other organ found amongst Invertebrate animals. The *meaning* of a part is an inference of the intellect. When exact, it is founded upon a correct appreciation of structure. A 'law' is upraised upon the basis of particulars. Let the following difficult inquiry be conducted in rigid compliance with this *regulus philosophandi*. Though abundant, the elder literature upon this subject has bequeathed little that is accurate and true. Baer* alludes in a special manner to the pectinated character of the branchiæ in the Lamellibranchiata; he illustrates his description by the gills of *Mytilus*. Meckel † depicts and describes in general terms a comb-like structure in the gills of *Spondylus, Pecten,* and *Arca*. Cuvier's figures and descriptions ‡ delineate the same formation. In his valuable notes, Siebold § describes the branchiæ in *Pectunculus, Mytilus, Arca, Pecten, Avicula,* and *Lithodomus* as consisting of a system of parallel vessels. In the text of his work, however, Siebold, like Mr. Hancock, speaks of the trellis-like network of the branchial structures. Among the older authors by whom allusion is made to the pectinated arrangement of the branchial vessels, the names of Bojanus, Treviranus, and Poli may be enumerated.

The contributions of Mr. Hancock upon this subject are the most recent, special, and distinguished ||. By this observer three types of structure are recognized. They are thus defined in his own language:—"There appear to be *three distinct modifications* of gill-structure in the Lamellibranchiata. In the first the laminæ forming the gill-plate are composed of filaments either free or only slightly united at distant intervals, as in *Anomia* and *Mytilus*; in the second they are formed by a *simple vascular network,* as in *Mya, Pholas,* &c.; and in the third the laminæ of the gill-plate are complicated by the *addition of transverse plicæ composed of minute reticulations of vessels,* as in *Chamostrea, Myochama, Cochlodesma,* &c. Other modifications may exist,

* Meckel, Arch. 1830, p. 340.

† Syst. der Vergleich. Anat. vi. p. 60.

‡ Règne Animal, nouvelle edit., Mollusques, pl. 74. fig. 2 *a*.

§ Anatomy of the Invertebrata, translated by Burnett, p. 211.

|| The excellent papers of Messrs. Alder and Hancock, to which repeated reference is made in the text, will be found in various Numbers of the 'Annals and Magazine of Natural History' for the years 1852 and 1853. To the attentive perusal of these valuable essays the student of the subject is earnestly advised.

but these are all that have come under my observation *." In each of these "modifications" one common character is said to prevail—the vessels *reticulate*—in the first only "slightly," in the others more "minutely." Such is the structural law of the branchiæ of the Lamellibranchiates as expounded by Mr. Hancock. It is at direct variance with the prevalent and accepted definition. Dr. Sharpey says—"Each gill (of *Mytilus*) or leaf consists of two layers, which are made up of vessels set very close to one another like the teeth of a comb or like parallel bars, &c.†" "These bars are connected laterally with the adjacent ones of the same layer at short intervals by round projections on their sides," &c.‡

Here this accurate observer conspicuously indicates the difference between the solid projections interposed between the vascular bands, tying them together into a horizontal lamina, and the "transverse plicæ" of Mr. Hancock, which transform a matchless system of parallel bars into one of "minute reticulation" (Hancock), which neither the eye nor the understanding can unravel. M. Deshayes § stands in this anomalous position:—he has figured accurately what he has interpreted wrongly. Albeit to this author merit is due. He has pointed out clearly by the pencil—what really exists in nature; what he himself misunderstood; what neither Dr. Sharpey nor Mr. Hancock seem at any time to have recognized—a structure without which the gill of the Lamellibranch could not architecturally be what it is; a marvellously woven fabric, refined in the utmost degree in its mechanism, adapted with incomparable skill to the purpose in view—a structure which no observer either anterior or posterior to the time of M. Deshayes has even suspected to exist—that apparatus of transverse scaffolding (Pl. VI. fig. 1 *c, c, d*) situated between the lamellæ of the gill, crossing at right angles the axes of the interlamellar water-tubes, *j, j* (of the existence of which M. Deshayes had not the slightest knowledge), and doubtfully described by him as the true *blood-channels* of the branchiæ! M. Deshayes mistook the laminæ formed by the real branchial vessels for "*membranous* layers or laminæ, *within the substance of which the branchial vessels* are arranged with great regularity." His *eye* caught with correctness nearly *all the parts* of this exquisite apparatus; his reasoning then enveloped them in

* Annals and Magazine of Natural History for April 1853.

† Art. "Cilia," Cyclop. of Anat. and Phys.

‡ This concise description is rendered still clearer by the original figures which accompany the famed article of Dr. Sharpey, to which I have adverted in the text.

§ See art. "Conchifera," Cyclop. of Anat. and Phys.

confusion*. Nothing less than a *rediscovery* of these skeletal parts, by which the branchial vessels are maintained *in situ* and the whole tubular system preserved in shape, could suffice to render complete and consistent the demonstration of the anatomy of the Lamellibranchiate gills.

With the eye stedfastly fixed on these parts, it is surprising that M. Deshayes could see in them no meaning, could read in them no purpose. In defining the outline and office of the inter-lamellar water-tubes, it is matter of wonder that Mr. Hancock did not suspect the mechanical *necessity* for a supporting apparatus such as this, without which the water-tubes could not sustain their patency or their form. Such is the history of progress in all the manifold paths of scientific observation. Discovery must literally be *prefigured* in the intellect of the thinking observer. In the absence of the foreshadowing conception, wondrous things in nature rendered manifest by accident are vacantly gazed at, left unfathomed, and then forgotten, or mentioned only as incidents or episodes in the drama. The merit which belongs to rediscovery is too often withheld from its author. It is morally, in equity, not less worthy of honour than the first discovery.

The law was formerly stated that the blood-channels in the gills of the Lamellibranchiate mollusks occur always in every species in form of straight, parallel, independent, non-communicating tubes, supported on the two opposite sides by hyaline cartilages, generally membraniform and semicylindrically curved (Pl. VI. figs. 6 & 6^2; and Pl. VII. fig. 15). These blood-channels never reticulate. At the free border of the gill the afferent channel returns into the efferent in a looping manner (Pl. VI. fig. 1 *e, f*). The efferent like the afferent channel preserves its individuality from one border of the lamella to the other (*m, e*). The blood-current, therefore, preserves unmixedly its singularity and independence from the beginning to the end of its branchial orbit (Pl. VIII. figs. 23 & 24). This is a striking and remarkable characteristic. It is a molluscan peculiarity. Its prevalence in this class is universal. It stands in contrast with the crustacean. The network plan is here the type. In some species of Annelids the branchial vessels observe a straight, parallel, looping mode of division. In the Annelid the blood is coloured and non-corpuscular. In the mollusk it is replete with globules. The blood-globules travel through the branchial 'bars' in a single series, or two abreast. In the crustacean the blood-channels are imparietal sinuses. In the mollusk each

* The reader is requested to refer to fig. 352, article "Conchifera," in the first volume of the 'Cyclopædia of Anatomy and Physiology.'

vessel is elaborately carved and wonderfully protected (Pl. VI. figs. 6 & 6²). The difference is as essential in kind as it is conspicuous: it may serve hereafter to establish the true direction of equivocal affinities. Subtle analogies, like deeply hidden differences concealed amid the profoundest recesses of the organism, are often more conclusive in disputative questions of specific and generic relationships, than diversities or resemblances graven prominently in the manner of the outward form.

In now entering upon the narrative of the minute structure of the gills in the conchiferous mollusks, it must be premised that illustrative types only can be comprehended in the story. Specific varieties and modifications must be left to the specific inquiries of individual observers. There prevails, however, such a remarkable uniformity in the architectural principle on which the breathing organs in all Lamellibranchiate mollusks are constructed, that departures from the central plan never involve a change of type. Such variations are apparent, not radical. Though a concise description, aided by illustrations, may enable the author to convey a readily intelligible statement of these parts, the reader must not infer that his task has been easy or his labour light. He has traversed dark and tangled controversies. For long he could pilot his course by the magnetism of no clearly-defined principle. Evidence conflicted, assertions bewildered; the subject was intricate, the clue of *principle* was wanting. He would fain trust that the history which he is about to write will transform a pre-existing chaos into the cultivated scene of exact demonstration.

The minute structure of the gills in the Conchifera may be conveniently described under the heads severally of the constituent parts of which they are formed.

1. The parallel bars or vessels forming the lamellæ.

2. The borders of the lamellæ, (*a*) attached, (*b*) free.

3. The transverse connective parts—intervascular, or intervectal.

4. The interlamellar water-tubes and the *intra-tubular framework* of support.

5. The ciliary system of the gills.

1. In the Acephalous mollusk the branchial vessel is sculptured upon one essential plan. All deviations from this plan are inessential varieties. So singularly do these blood-canals differ from ordinary blood-vessels, that they will be henceforth described under the name of "*branchial bars.*" The word 'bar' implies, first, straightness, and secondly, rigidity, two properties which belong to the branchial bars. The word 'bar' involves the idea of separateness, individuality and independence—characters which apply to the branchial bars. Rigid bars arranged

in parallel directions on the same horizontal plane would form a *stratum of bars*—such is the branchial lamella. Disposed on two coincident planes, one above the other, two parallel lamellæ would result. Between parallelly-arranged rigid bars the *inter-spaces* would be parallel and equal—such are the *intervectal* * water-passages of the branchiæ. If traversed by cross threads at frequent intervals, a long fissure would assume the form of oblong foramina (Pl. VI. fig. 1 *g*, fig. 2 *e*). Such sometimes are the varieties which occur in the intervectal passages. If the parallel lamellæ be tied together at regular points by bands running with the bars, the space between the lamellæ would be divided into tubes. Thus are formed the interlamellar water-tubes (figs. 7, 9). The picture is faithful to nature. It mirrors the reality of a complex apparatus. It represents in simple outline the machinery of the branchiæ in the bivalve mollusk.

The details are now neither intricate nor unintelligible, because the *constructive idea* is clear to the intellect. In all investigations a tangibly-grasped *mental* picture must forerun the clear perception of the outward reality.

A branchial bar is a *tube* whose sides are comparatively rigid, and whose diameter is uniform (Pl. VI. fig. 6 *a, a*). It is clothed externally by a membrane, the continuation of the mantle, of which the epithelium is evolved at certain regular lines into cilia-bearing scales (*b*). The opposed sides of each bar are formed of, and supported by, cartilages (*a, a*). If these two cartilages were far removed apart, the blood-channel would be broad and flat (Pl. VII. fig. 15 *b, b, b*). These cartilages are slender in the extreme in texture; they are membraniform and exquisitely hyaline; curved at the edges, they assume the figure of a hollow semicylinder; they possess just enough rigidity to preserve the straightness of the bar; they are *continuous* throughout the whole length of the bar (Pl. VIII. fig. 17). Being placed on the opposed horizontal sides of the bars (not on the upper and under aspects), they must necessarily circumscribe a tubular channel of unbroken continuity. The sides are not perforated by openings of any description. If the transverse structures (Pl. VIII. fig. 22 *a*), afterwards to be described, be *vessels* or blood-channels, as conceived by Mr. Hancock and some of the elder anatomists, the bore of such channels cannot communicate with that of the parallel bars. The transverse parts must therefore, if they be blood-channels at all, constitute an independent system. But they are *not* so. They are con-

* From the Latin *vectis*, a bar. Since it is proposed to distinguish the branchial blood-channels under the name of bars, it is only consistent to mark the spaces between them as *intervectal*, rather than as intervascular.

nective fibrous structures (Pl. VIII. fig. 19). In almost all species of bivalve mollusks, the branchial bars more or less closely approach the cylindrical in figure. To this rule of structure those of the common Mussel form a remarkable exception: they are here blade-shaped (figs. 17 & 20). The section of the bar is frequently oval. In the genera *Cardium, Unio, Ostrea,* &c. this form is exemplified. The subcylindrical canal, circumscribed by the hyaline cartilages just described, is the true blood-channel*. All naturalists have conjectured this fact; the existence is now only for the first time *proved.* The cartilages bounding these channels are now first announced. They do not enclose the whole circumference of the vessel: they form a third of the opposite halves (Pl. VI. fig. 6^2). The rows of cilia correspond with their edges: the intervals between these edges are membranous. The real osmotic movement of the gases concerned in respiration is limited to these intervals. Along these intervals, extending with beautiful regularity from one end of the bar to the other, there travels a cilia-driven current. In *Mytilus* the bars appear to swell (Pl. VIII. fig. 17 *o, o, o*) at the points at which they are joined together by the transverse structures. The real blood-channel does not bulge. The cartilages of the bars at the base of the lamella are lost in and identified with that embracing the trunk common to the whole series (*c, c*). Traced carefully to the proximal border, they will be observed to have this disposition: the cartilages of contiguous sides of *adjoining* bars form one piece, being so bent as to become continuous at the proximal border of the lamella. The bars are thus held firmly *in situ* and in relative connexion.

At this point it becomes extremely interesting to inquire, whether the *lamella* is composed of a single series (Pl. VI. fig. 4), laid side by side, of parallel bars, or of a double series arranged in two separate planes? (fig. 5). The answer to this question will implicate an important point of function. It is difficult to convey clearly the idea of a double series of bars constituting a *single* lamella. This undoubtedly is the disposi-

* A very recent study of the minute structure of the gills in the Tunicates and Ascidians has enabled me to resolve completely the homology of the *branchial bars* in the bivalve mollusks, to explain demonstratively why it is that in the gills of some Acephalans the blood-conduits are placed like membranous channels between *alternate bars* (as is shown in Pl. VII. fig. 15, *b, b, b*), and that in others the blood-canal (as in Pl. VIII. fig. 22) occupies the *axis* of each bar. Though there exist in the gills of the Tunicata a system of large *transverse* trunks, with which the *parallel* ultimate blood-channels (the homologues of the "bars" in the Acephala) openly communicate, in *a supplementary note on this subject* in the next paper, it will be shown that the ultimate elements of the branchiæ in Tunicata and Acephala are really arranged on the same type.

tion of the branchial bars in some species of Acephala. If a "bar" be bent once upon itself (fig. 3), and if then one limb only be rested upon a flat surface, the other limb will be on the same vertical plane, but on a different horizontal plane. If a second, then a third bar, and so on, be placed in coincident directions, the limbs will form two horizontal series or laminæ, between which a free undivided horizontal space will exist (*e, f*); but there will also exist vertical spaces between each two adjoining bars having the same vertical planes. In words this arrangement is complex, in illustration simple. Now it may at first be supposed that of mechanical necessity this must be the order in which the bars are arranged in all the examples of double gills* (Pl. VI. figs. 1 & 7), as it is really that in which the afferent and efferent limbs of the same looped bar are disposed in all instances, without exception, of *single* (Pl. VI. fig. 2) gills. But it is truly the case only in a very few genera. It is so in the Mytilidæ (Pl. VIII. fig. 24). It follows that under the latter circumstances the interlamellar water-tubes must be bounded by two concentric walls (Pl. VI. fig. 5), each wall being composed of a single horizontal series of bars. Of this disposition another apparent example is afforded in the Ostreadæ; if the disposition of the loops at the free margin *only* be considered. In nearly *all* other genera, known to the author, the limbs of the same looped bar are placed on the same horizontal plane (Pl. VI. fig. 7 *f*). The plane of the loop notwithstanding at the distal border of the lamella is not horizontal, but vertical. It results that each lamella is composed of a single series of bars, though the contiguous limbs alternate in function, one conveying a centripetal, the other a centrifugal current (Pl. VII. figs. 9 & 11). But it must be remembered that a single lamella (*a* or *b*, Pl. VII. fig. 11) of a double gill is not the exact equivalent of an entire single gill (fig. 14). In *all* single gills the limbs of the same bar rest on vertical planes; those of a single lamella of a double gill are placed on the same horizontal plane (fig. 12). In the single gill the physical conditions are more favourable to the complete aëration of the blood. The water-currents are different, not the same. It will greatly facilitate the comprehension of the preceding history if now *the minute anatomy of the free or distal borders of the branchial lamella be carefully and accurately studied.*

The structure of the extreme free edge of the lamella furnishes a ready key which unlocks at once the whole mystery of the branchial apparatus; and yet this wondrous part of the organ

* The meaning attached in these papers to the *double* as opposed to the *single* gill is afterwards explained.

has never arrested the curiosity of the anatomist. In *Mytilus* and in *Mytilus* only, Dr. Sharpey figures correctly the manner in which, at the distal margin of the lamella, the bars of the upper become continuous with those of the lower lamella. In *Mytilus* the structure of the gill is almost unique (Pl. VIII. fig. 17). The order which obtains in nearly all other genera could not be deduced from the anatomy of the Mytilidan gill. It is a singular exception. It is the rare exception only that Dr. Sharpey has pictured. The *rule* of structure remained really to be discovered. If the blunt and acute edges of the penknife-shaped branchial bar (fig. 20) carry each a blood-channel, then each *gill* in *Mytilus* will be a double gill, for the upper and lower are identically formed. If, on the contrary, the blood-channel exists only at the blunt edge (*a*) of the blade, the current travelling peripherally along the bars of the upper lamella (A, fig. 17) must turn round (as shown in fig. 24 *d, d*) at the free margin through the loop and move centrally along the bars of the lower lamella (B, fig. 17). In the latter case the gill would be single, in the former double. The bars of the upper lamella when the gill is single carry currents moving in the same direction (Pl. VI. fig. 2; Pl. VII. fig. 14) from one border of the gill-plate to the other; those of the lower, oppositely tending currents (Pl. VIII. fig. 23 *e, f*). This point is the wonder-striking feature of the branchial enginery. No writer has ever given to it a single thought. It deserves to be further elucidated. In *Pholas* (Pl. VI. figs. 1 & 2), *Gastrochæna, Mya, Tellina, Mactra, Cypræa, Cardium* (Pl. VII. figs. 13 & 14), *Ostrea* (Pl. VIII. fig. 21), and probably in many other genera, the inner gill is *double* and the outer is *single*. The Pandoridæ and Lucinidæ are families in which the outer gill is altogether suppressed. In *Solen, Pecten, Unio, Venus, Kellia, Arca,* &c., the two gills on both sides are equal in size and *double* in structure.

Every gill-plate, whether single or double, is composed of two lamellæ, between which the excurrent water-tubes (see large arrows in Pl. VII. fig. 13, Pl. VI. fig. 1, and figs. 7 & 8) are situated. In the example of the double gill *each lamella* is the scene of a double system of opposed currents of blood, since the two limbs of the same looped bar lie on the same horizontal plane in the same lamella (Pl. VII. fig. 9 *c*). The adjoining limbs are thus alternately afferent and efferent, or venous and arterial. *Each lamella* then of every double gill is a complete and independent gill. Its system of circulation is distinct, and totally unconnected with that of the other lamella. Neverthe-less, a single lamella of a double gill is not identical in ana-tomical characters, or structurally, or perhaps officially, equivalent to an entire single gill. As formerly intimated in the example of a single gill, the limbs of the same looped bar, respectively venous and arterial, are placed on different horizontal planes (Pl. VII. fig. 14), the planes of the *loops* (*a*) at the free margin being vertical, and not horizontal as they are in general in the double gill (Pl. VI. fig. 1; Pl. VII. figs. 9 & 11). The single gill, like the double, is composed of two lamellar planes (fig. 14 *b*, *c*) bounding intermediate water-tubes. But in the single gill each lamella is single in function, since it consists of the afferent or efferent limbs separately and exclusively of the looped bars. In either lamella therefore the adjacent bars belong to separate and independent loops. The component bars of the lamellæ in all single gills are separated from one another by intervectal water-fissures (Pl. VII. fig. 15 *c, c, c*). In the double gills in which the two limbs of the same loop lie adjoined on the same horizontal plane, such limbs are united together by a *continuous membrane* (Pl. VI. fig. 5). In such case the intervectal water-fissures exist only between the limbs of different contiguous loops, not between those of the same looped bar. By this arrangement the volume of water which traverses the gill at any given time is reduced by exactly one-half. The functional value of the organ therefore sinks in the same degree. A *double* gill (Pl. VII. figs. 13, 9 & 11; Pl. VI. fig. 1) in structure is not necessarily twofold in physiological import. In official activity it exceeds little the single gill. In the latter the blood is more intimately brought into contact with the respiratory medium, and this medium is more readily and rapidly renewed. To the single gill (Pl. VI. fig. 2; Pl. VII. fig. 14) conchologists have applied the term *supplementary*. It is difficult to understand in what sense this term should be received. In *structure* the single gill is *not* supplementary. It is a perfect and complete organ. No constituent element is deficient or suppressed. In function it is complete. It is not a supernumerary organ. Both these designations are significant of what is untrue. It is as much an integer of the organism as the upper or inner gill. A *law* hitherto undiscovered does, however, affect the presence and dimensions of the outer or single gill which does not influence the inner or double gill. If, as in the Pandoridæ, Lucinidæ, and some other families, there exist only one gill, it is invariably the single or out-gill that is wanting. The principle of suppression or non-development affects exclusively the latter. When only one gill exists, that is, one on either side of the foot and body, it is always *double* in structure. It contains the same number of bars and loops as any other double gill. It is quite erroneous to conceive that in such a case the absent or suppressed gill has been fused into and identified with the present solitary gill. The latter is the same in essential structure as if the single gill were present.

In *Pholadomya* and *Anatina*, Professor Owen describes the two branchial lamellæ of either side as having been united to form a single gill*. Valenciennes states that the solitary gill of the family Lucinidæ resembles that of *Anodonta*; it is larger, and formed of thicker and more prominent pectinations. *Lucina Jamaicensis, L. tigrina, L. columbella,* and *L. lactea,* are examples in which only a single branchial organ exists on either side. The solitary gill differs from the ordinary double gill only in *apparent* characters. The free border is composed only of two rows of loops; but these loops are soldered together by an obvious longitudinal band or cord, running in shape of a deep water-groove from one end to the other of the free margin (Pl. VI. fig. 3 *b*). It is this character which occasions the appearance of doubleness and fusion. In the solitary gill of the Pandoridæ and Lucinidæ, the pectinations† of the lamellæ are coarse and large to the naked eye. This circumstance is due to the greater size in these cases of the interlamellar water-tubes. It is repeated, that the vascular elements, in the solitary gills, are the same in number and disposition with those of any other double gill. If, in the example of the solitary gill, the outer single gill were really organically united to the inner double gill, an organ should result consisting at the free border of *three* rows of vascular loops, *two* distinct systems of parallel interlamellar water-tubes, *four* separate lamellæ, *three* layers of afferent and *three* of efferent bars! Such, of mechanical necessity, should be the anatomical characters of a gill which owed its formation to the union of one already double to another struck on the single plan. Such a monstrosity is not illustrated in nature. It is a fabulous branchia, born of hypothesis. But it *may appear* quite reasonable to explain the anomaly of a solitary gill, on the supposition that it is the natural and necessary product of the fusion of two *single* gills. A glance at the illustrations depictive of the type of the latter, will at once convince the mechanician that two single gills could not in any manner be fused in order to make a double gill,—such a double gill, that is, duplex in mechanism, twofold in function, as actually exists in the real animal. Let two single gills be brought together (Pl. VI. figs. 7 & 8),—the water-movement and the ciliary action would cease at once on the two adjoined, apposed faces. Thus the power of each would be reduced by one-half. Two singles united make a single! Such is the clumsiness of human handi-

* Forbes and Hanley, British Mollusca, vol. ii. p. 42.

† It should be distinctly understood, that the word '*pectinations*' is not synonymous with an ultimate branchial bar, but with that *set* of bars which form an interlamellar water-tube.

craft: attempting to mimic nature, it is lost in caricature. Nature does not reach her ends by the "fusion" of organs. An existing organ is *modified* to fulfil a collateral purpose. A solitary gill has its own peculiar characters. The component vessels remaining unchanged in number and arrangement, a solitary organ is rendered equivalent to a double one, by augmenting the dimensions of the passages and tubes in such a manner, that the aërating element brought into relation with the blood can be increased almost to any amount. *Function* is thus intensified, while structure remains analtered.

The *loops of the vascular bars,* as they project at the free margin of the lamellæ, are differently joined and variously figured and sculptured in different genera, and frequently in different species of the same genus. In *Pholas* (Pl. VI. figs. 1 & 4), the free border of the double or inner gill presents two rows of loops (*e, f*). The plane on which the loops of the upper lamella rest is horizontal, coinciding with the *length,* as opposed to the breadth, of the gill. Those belonging to the lower lamella of the same gill, form a row on a plane an eighth of an inch below the former. Between these two projecting scalloped edges, a groove (fig. 3 *b*) runs from one end of the gill to the other. The cilia which fringe this groove (Pl. VIII. fig. 24 *h*; Pl. VII. fig. 10, *a, b*) are very much larger in all species than those which are distributed over the bars at the plane faces of the gills. They excite a vigorous current, bearing towards the mouth. Those of the flat surface (Pl. VIII. fig. 20; Pl. VI. fig. 6 *b, b*) raise streams, tending towards the free border of the gill. Both are subservient to alimentation and respiration. In *Pholas,* then, the double gill (Pl. VI. fig. 1) is composed only of two lamellæ, like the single gill (Pl. VI. fig. 2); but in the former, each lamella is composed of two orders of bars, in the latter of one order only. The two limbs (fig. 4 *b, b, c, c*) of each looped bar in the former are placed on the *same* side of the intermediate water-tube: the afferent and efferent limbs of the same bars (fig. 2 *h, f*), in the instance of the single gill, are so *opened* or separated at the free margin as to form respectively the *opposite* walls of the included water-tube. The vascular *loops* at the margin of the double gill in nearly all genera are disposed flatwise (Pl. VI. fig. 1 *e, f*; Pl. VIII. fig. 21 *c, b*; Pl. VII. fig. 9 *a, b,* fig. 11 *a, b*), so that all the loops of the same lamella form one horizontal plane. Those of the single gill (Pl. VII. fig. 14 *a*; Pl. VI. fig. 2) are placed vertically, so that the plane of each loop is separated from, though parallel with, that of the adjoining loops. In the double gills of the Cardiadæ an exception occurs, and probably in other families. The loops at the distal margin are disposed here on vertical planes (Pl. VII. fig. 14 *a*); but though standing vertically, they do not enclose two systems of interlamellar water-tubes, but only *one*. The *mechanical* problem presented by the gills of *Cardium* proved extremely difficult of solution. *When understood*, it challenged any living mechanism for beauty and perfection. In *Mytilus* the loops of the two lamellæ are soldered into union at the free borders: they stand vertically (Pl. VIII. figs. 17 & 24): they circumscribe a deep intermediate gutter. In *Solen* (Pl. VIII. fig. 23) the loops expand. In *Venus* they also somewhat exceed in diameter that of the bars, of which they are *the bend*. In *Mytilus*, the inner and outer gills exhibit the same formation. In the Ostreadæ (Pl. VIII. fig. 21), the loops at the margins of the gills are so closely packed together horizontally, as to appear like a continuous membrane bounding an angular groove. Numerous other varieties in the mere shape and size of the loops occur in different families of Bivalves—the *type* of structure never changes.

The proximal or attached border (Pl. VI. figs. 1 & 2 *a*, *b*) of the gills occurs under many varieties of anatomical plan. *Pholas* exemplifies one type. The two lamellæ* are attached to the pallial tunic. All the vascular bars terminate in a common trunk (Pl. VI. fig. 2 *a*, *b*) which runs at right angles to their axes, and parallel with the length of the entire gill. There are two of these trunks, one afferent, the other efferent. They occupy respectively the proximal margins (Pl. VI. fig. 1 *a*, *b*) of the two lamellæ of which each gill is composed. In *Pholas* these trunks are supported by the framework of *solid* structure (*c c* and *d d*) which occupies the interlamellar spaces. In *Solen* (Pl. VIII. fig. 23 *a*) and *Mytilus* (fig. 17 A) another plan of formation is observed. Here the proximal border of the superior lamella of the upper gill, and inferior lamella of the under gill, are *unattached*, floating in the mantual cavity. In such instances the interlamellar framework is wanting. The vascular bars at this border, for some distance up the breadth of the gill, are tied together by means of a *continuous* membrane (*e*, *e*). Here the interlamellar scaffolding, and the water-tubes which the former assist to form, exist only where the two lamellæ are adherent; viz. over the two-thirds of the breadth of the gill nearest the free border.

* It should be clearly explained that the word *lamella*, as applied to the gill of the Acephalan Mollusk, should signify, *one* of the two plates of which the gill, whether double or single, is composed. The gill is the whole organ. In those instances in which (as shown in fig. 5, Pl. VI.) the bars stand vertically on the same lamella, then of course each lamella would be composed of two plates, or finer lamellæ. I am not quite certain that such an arrangement exists in nature. In several genera—in *Cardium* especially—when care is taken to avoid *pressure* upon the margin, such is the true position of the loops, if not of the bars proceeding backwards from them.

Intervectal and Interlamellar Framework of Connective Structures.

These structures constitute the true skeleton by which is sustained the vascular fabric of the gill. Of the latter, they determine the shape and the form. They preserve the blood-carrying bars in position. They hold apart the component lamellæ of the gills. They thus *form* the interlamellar tubes, since without these structures the lamellæ would fall together into contact and obliterate the tubes. Messrs. Alder and Hancock recognized the tubes, but overlooked the framework system by which they were constructed *. M. Deshayes has *figured* this framework (Pl. VI. fig. 1 *c, c, c* & *d*, fig. 2 *i*, and fig. 8 *d, d*) apparatus in a conchiferous (*Pecten* or *Arca*?) mollusk. Not a sentence is written descriptive of its characters, or interpretative of its meaning †. Attention was drawn to it by no allusion whatever, direct or incidental. Philippi ‡ has this observation with respect to the branchiæ of *Solenomya*, which probably refers to the interlamellar structures in question:—"Branchiæ duo non quatuor, non lamelliformes, sed pectinatæ vel potius pennam exacte referentes, lamellis transversis perpendicularibus, carina media corpori per totam longitudinem adnatæ, versus apicem *ope ligamenti*." Ill-defined reference to the same parts is made by Carus, Blainville, Garner, and others. To be known descriptively, and comprehended physiologically, they remained really to be rediscovered,—to be read by a *new* eye, from

* It is very probable, from the following passage, that Messrs. Alder and Hancock have mistaken the thick solid cords which at short intervals cross the *tubes*, for real blood-channels: "The laminæ forming the walls of these tubes were now examined through the microscope, when the whole was observed to present a regularly *reticulated* structure composed of blood-vessels; *those passing transversely being the stronger and more prominent*."—Annals and Magazine of Natural History, paper on Currents in *Pholas* and *Mya*," 1852.

† The following is the only passage which occurs in the excellent article (Conchifera, Cyclop. Anat. Phys.) of M. Deshayes having reference to the structure of the gills:—"In the greater number of genera, the branchiæ are formed of two membranous layers or laminæ (*a, b*, fig. 352), within the substance of which the branchial vessels descend with great regularity. In several genera, as the *Archidæ* and *Pecten*, the branchial vessels, instead of being connected parallel to one another *within the thickness of a common membrane*, continue unconnected their entire length, and they are thus formed of a great number of extremely delicate filaments, attached by the base within the membranous pedicle on which the branchial veins pursue their way towards the auricle." Nothing is said of the distinct and independent structures which separate the laminæ. The condition, namely the *separation* of the laminæ—upon which depends the existence of the interlamellar water-tubes—is here *accidentally* stated; but neither the existence nor the meaning of such parts seem in the slightest degree to have been imagined by M. Deshayes.

‡ Moll. Sicil. i. p. 16.

a *new* point of view. The author believes that the following is the first systematic exposition on record of the anatomy and significance of the *non*-vascular elements of the lamellibranchiate gill.

They are classifiable under two heads. Those parts which are placed between (Pl. VI. fig. 1 *g*, fig. 2 *e*, fig. 8 *d*; Pl. VIII. fig. 19 *c, c, c*) the parallel bars (*the intervectal*), uniting them into the form of a leaf, constitute a separate order. Those, *secondly*, stronger, coarser, in some genera very conspicuous, in others very concealed, which separate the lamellæ, forming and bounding the excurrent interlamellar water-tubes, to which in many species the ova adhere, the basis of the whole gill, the wonder of the whole enginery, the last of the branchial constituents to be described and understood, are really a distinct and unknown class of structures.

The first class vary the apparent anatomy of the gill more than the second. They cut the fissural spaces (Pl. VI. fig. 7 *d*) between the individual bars, or individual loops, into oval stigmata (fig. 5 *d*), elliptical perforations, or lengthened parallelograms (Pl. VII. fig. 12 *d*). In the absence of them, as in *Thracia* (Pl. VII. fig. 15), the intervectal water-fissures are continuous from the free margin of the gill to the proximal. In *Mytilus* (Pl. VIII. fig. 17 *o, o, o*) they appear under the character of fleshy nodules; in *Cardium* (Pl. VII. fig. 12 *c, c, c*) they are almost invisible; in the Veneridæ they consist of a flattened bundle of slender threads, running from bar to bar at equal intervals; in *Pholas* they assume almost a membranous form (Pl. VI. fig. 4*e*), perforated at regular distances by oval holes; they exist only between alternate loops. In a physiological sense, the highest value attaches to these intervectal parts. They determine the dimensions of the water-stigmata. If they are small, the water of respiration is very much subdivided; if large, the lamella is readily traversed by the aërating element. In calculating the quantum of respiration in the Conchifera, *two factors* demand to be estimated: first, the amount of blood entering the breathing organ; secondly, the volume of water by which, in a given time, it is capable of being traversed. The latter will depend upon the dimensions of the water-passages.

The intervectal connective structures have been mistaken for half a century by the best observers for *vessels, blood-canals crossing the bars*,—deceiving the observers into the idea that each lamella in the lamellibranchiate gill is really composed of a *network of blood-vessels*. This idea as regards the Acephala involves a fundamental error; it envelopes everything in unresolvable confusion. The orbit of the branchial circulation cannot be explained. It contradicts the anatomical arrangement conspicuous in other parts. A consistent sentiment cannot be shaped of this most perfect mechanism. They are *not* blood-channels. They are elastic, fibrous structures, enacting a purely ligamentous part. They derive their supply of blood from that of the branchial bars. Their office is mechanical, not chemical.

The *intra-tubular structures* (Pl. VI. fig. 1 *k, k, k*, fig. 8 *d, d*; Pl. VIII. fig. 21 *f*, &c.) are neither less remarkable nor less important. Upon this interlamellar framework depend the whole characters of the gill. They hold the lamellæ apart at *definite* distances. They unite closely together the loops of these lamellæ at the free margin (Pl. VI. fig. 7 *a, b*); thus they *close up* cæcally the tubes at this border of the gill *. This single point of structure is the pivot whereon turns the action of the gill. If the tubes at this extremity were open (as suppositionally at Pl. VII. figs. 9 & 11), it is hydraulically certain that the water would take this course to pass from the extra- to the intra-branchial cavity; none would pass between the bars which contain the blood; the function of respiration could not proceed; and this calamity, further, would ensue—no food could be carried to the mouth. Men do not value health until it is lost! Spectators see not, *feel* not, the perfection, the unimprovableness of organic mechanism until an element is ideally removed—until some deviation from nature's method of working is *supposed*! The *argumentum ad absurdum* startles by the bungle and foolery which it is sure to introduce; *then* philosophers realize the inimitableness of her certainty and refinement.

As the proximal borders of the lamellæ (Pl. VI. fig. 1 *a, b*) are separated by the whole diameter of the water-tubes, and as the distal margins are fused together, it follows that these tubes, like rivers, are small and shallow at their commencement, deep and broad at their termination. This arrangement favours their *suctorial* action. The water, as first explained by Mr. Hancock, is undoubtedly *drawn into* (properly *pushed* into) these tubes through the lamellar stigmata (Pl. VIII. fig. 17 *f, f, f*) from the pallial cavity. The water is discharged from the tubes by ciliary agency, which is constant (arrows in Pl. VII. figs. 9, 11, 13 & 14). They are thus constantly being emptied. If they were not refilled from without, they would become *vacuous*. During the action of the gill, there is momentarily generated a tendency to a *vacuum*. The pressure that is on the tubular side of the

* In the accompanying illustrations, in several instances (Pl. VII. fig. 9 & 11, Pl. VIII. fig. 21), these tubes are represented as if they were *open* at this margin of the gill. This method of illustration was adopted only for the sake of clearness, and in order that the disposition of the loops and bars of each lamella may be readily understood. In all cases, without a single exception, the tubes are *closed* at this border of the gill by the apposition of the loops of the two constituent lamellæ.

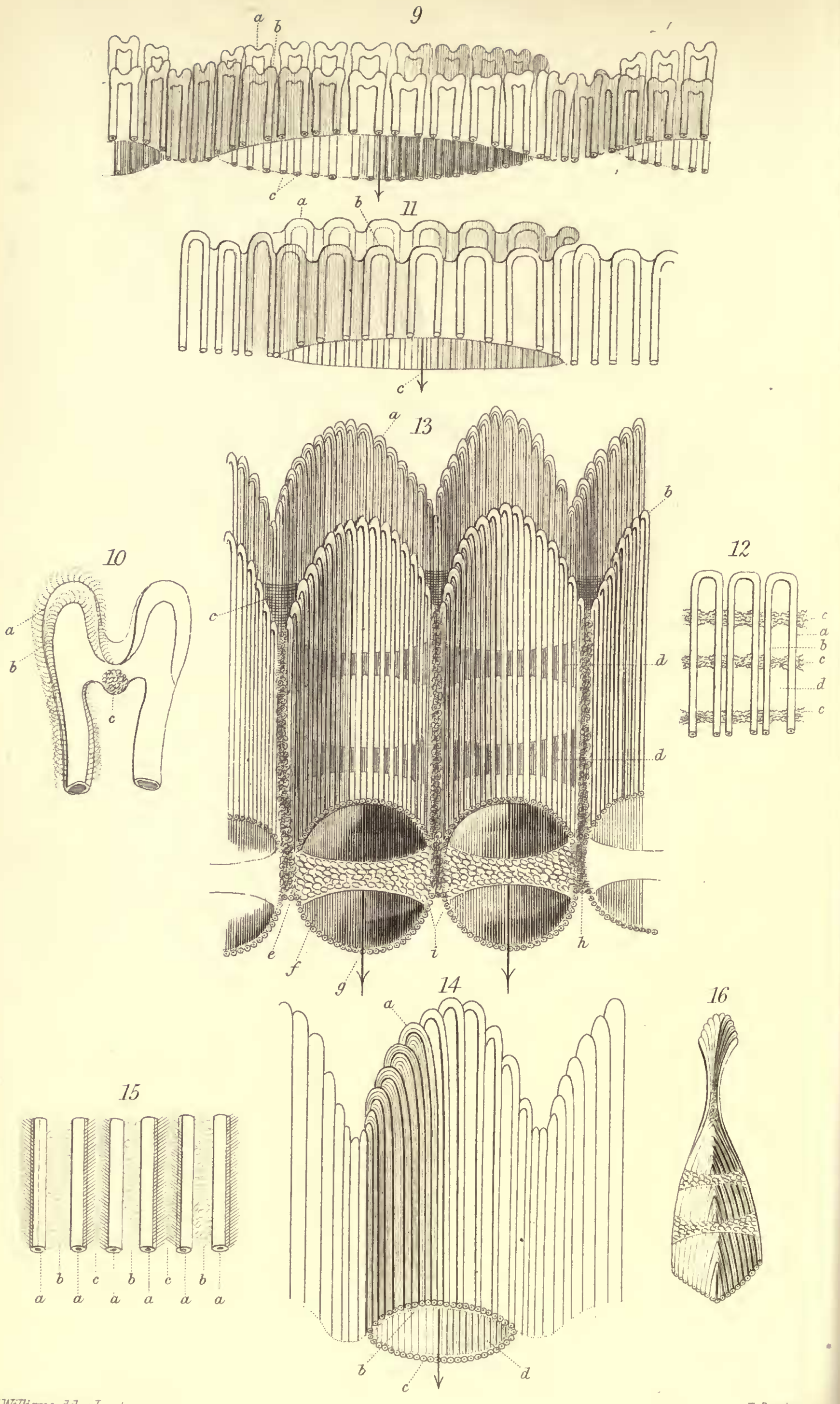
lamella is diminished; on the other it remains the same as long as the animal continues in the water. It is hydraulically inevitable, even *without* the assisting agency of cilia, that the water must transude the lamella by way of its intervectal fissures and perforations. This mechanism could neither be conceived nor explained before the nature and office of the interlamellar framework were brought under clear demonstration. It is important to understand, that that surface of the lamellæ which faces the intermediate tubes, namely the *internal* walls (Pl. VI. fig. 8 *e*) of the water-tubes themselves, is far less richly ciliated than the external surface. The excurrent movement of the respiratory water is much aided by the action of the connective structures of the bars and tubes. The intervectal pieces—those which pass crosswise from bar to bar by approximating the latter—are capable of stopping up the intervectal stigmata,—of suspending, therefore, the act of respiration. Thus is prevented the passage of irritating substances through the branchial lamella. The alternate movements of the shutting and opening of the bars is as important to the sieving operation of the gill, its prehensile function, as the cilia themselves. The transverse intervectal pieces (Pl. VII. fig. 12 *c, c, c*; Pl. VIII. fig. 19 *c, c, c*) consist of irritable and contractile tissue. They are capable, in part, of voluntary contraction. Thus, although the chemical act of breathing is in itself uncontrollable, it may be interrupted by the exercise of those connected parts which are subject to the will.

The skeleton of *solid* pieces (Pl. VI. fig. 8 *d, d,* fig. 1 *c, d,* fig. 2 *i, j,* &c.) by which the *tubes* and the *lamellæ* are supported and held apart, exists probably in the branchiæ of *every lamellibranchiate mollusk.* It constitutes a framework system, though anatomically distinct from, having a mechanical action concurrent with, the intervectal. At the free border this interlamellar substance is thin, slender, and difficultly detected by the eye, admitting of the falling together of the lamellæ and of the closing of the tubes. At the opposite attached border, the interlamellar substance is much thicker, coarser, and more conspicuous (Pl. VI. fig. 1 *k, k, k*); the parts being quite apparent *through* the lamellæ. Here, therefore, the lamellæ are further separated, and the tubes of the greatest diameter. This framework consists of two distinct pieces,—those, first, which run parallel with the vascular bars (Pl. VI. fig. 1 *c,* fig. 2 *i*); and, secondly, those which transversely connect these longitudinal pieces (fig. 1 *d,* fig. 2 *j, j*). The former limit the breadth of the interlamellar water-tubes. The tubes are capacious when the lamellæ are far apart, small when they are near each other. As the exterior appearance of "pectinations" in the gill is due to the presence of these tubes, the pectinations are obvious, as in *Cardium, Solen, Pecten, Thracia,* &c., when the tubes are large, invisible to the naked eye when they are small. The *cross pieces* tie together the longitudinal at regular intervals. The latter run with the tubes, and *divide them* from one another, the former cross them. If the transverse pieces were so thick and large as to fill up the tube, and interrupt its continuity, the ex-currents of water of course would be arrested, and the function of the gill would be suspended. It is far otherwise. They traverse the tubes in form of cords. Their extremities are attached to the opposed points on the horizontal sides,—to those very lines along the sides of the tubes at which the chemical act of breathing is passive. From this arrangement there flows this most beautiful result: the water, having permeated the lamella and gained the *interior* of the tubes, in its course towards the ex-current siphon, *is made to keep continually in contact with the branchial bars*. By this simple arrangement, the *two* sides, in fact the four sides, of each individual blood-carrying bar are *persistently* embraced by a moving current of the respiratory element! If the cross cords did not exist, every drop of water which entered the tube would collect at the most depending side, and flow out as *a useless and unused stream*. In the œconomics of nature, the subtlest œconomist may well marvel at her care!

The long pieces of this interlamellar framework are capable of shortening the length of the water-tubes, the cross pieces of diminishing their diameters. These actions impel, interrupt, facilitate, &c. the breath-giving currents. While they complicate the branchial machinery, they double the certainty of the process; they provide against accidents; they preserve in the required position the slender, tender, beautiful parts of which the apparatus is composed.

Endless diversities occur, in different species and genera, in the size, the figure, the visibleness, &c. of this interlamellar framework. In no single instance is there observable the slightest departure in *principle* of structure, in intention, in purpose, from the typal plan unfolded in the preceding description.

The *cilia-bearing epithelium* (Pl. VI. fig. 6 *b*) of the branchial lamellæ in the conchiferous bivalves is well known. It has been well described by trustworthy observers, from Leeuwenhoek to Quekett. The cilia in all cases are distributed in rows on the bars (Pl. VII. fig. 15; Pl. VIII. figs. 20 & 22). There are two rows on each external hemi-cylinder of each bar. On the *external* aspect of each bar, therefore, there are four lines of cilia (Pl. VII. fig. 10 *b, a*). They drive two currents in intersecting directions. On the interna aspect of each bar, that namely which faces the



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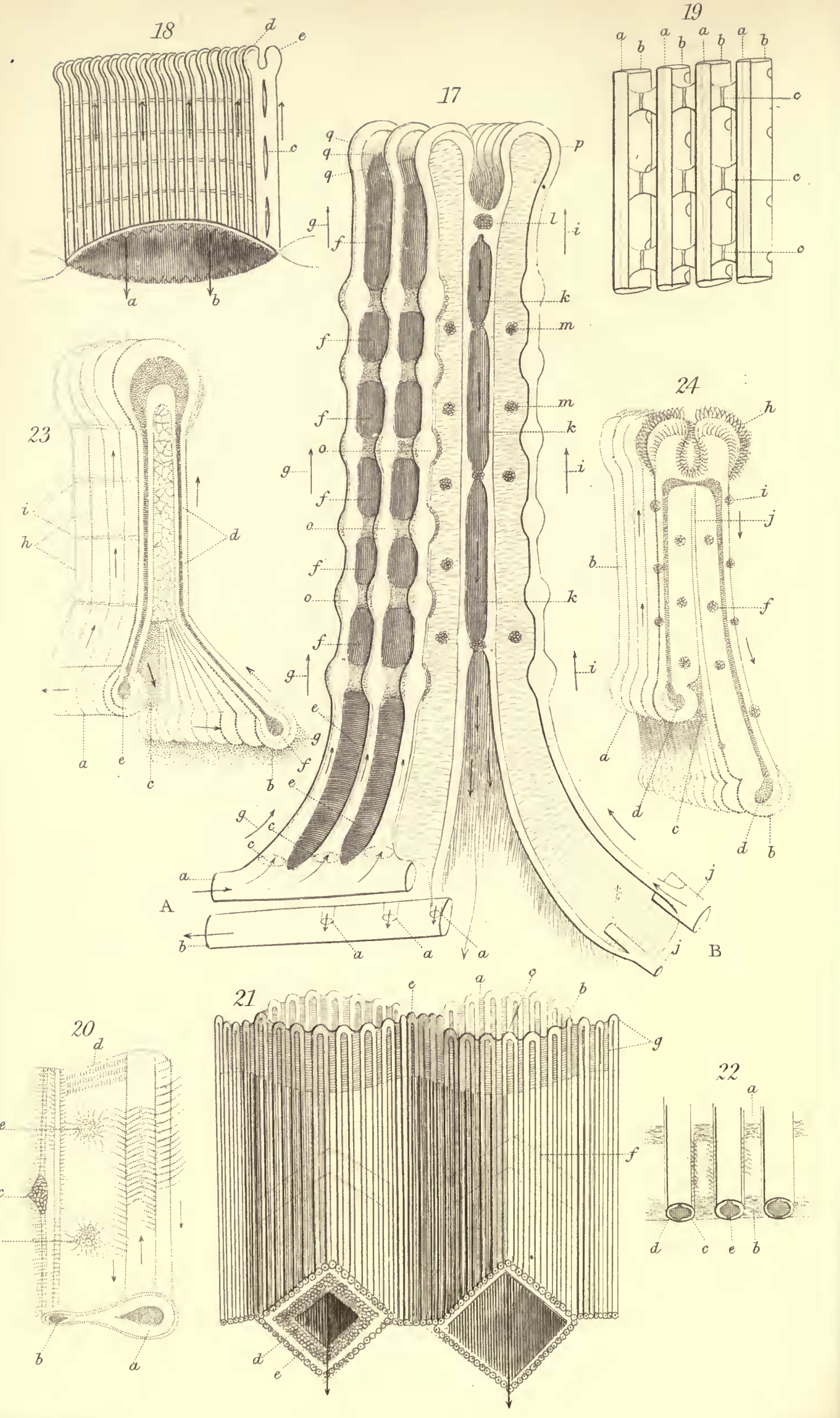

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